



Plants associated with wild pig (*Sus scrofa*) foraging activities in Singapore secondary forests

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Abstract

Wild pig (*Sus scrofa*) populations in Singapore have been rising over the past two decades, likely due to a lack of hunting or large natural predators to regulate their numbers, in addition to the availability of suitable habitats to expand into and possibly supplemental food from anthropogenic sources. In other nearby Asian forests, high densities of wild pigs have been shown to inhibit forest regeneration through seed predation, trampling, foraging for food (i.e., digging or rooting),

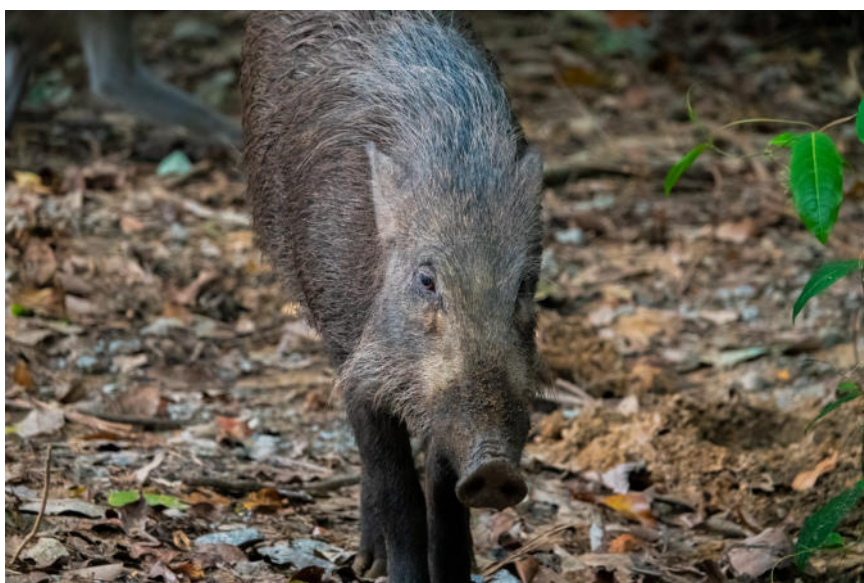


Fig. 1: A wild pig (*Sus scrofa*) in Singapore with traces of foraging (soil disturbances from rooting behaviour) in the background. Photo: B. S. Yap.

creating wallows, and building birthing nests, which all may damage seedlings and saplings. Wild pigs may also facilitate the spread of invasive species by causing soil disturbances or acting as seed dispersers. Here we assessed the plants associated with pig foraging sites in Singapore along eight 6 m (W) × 1000 m (L) straight-line transects in secondary forests. In contrast to many studies elsewhere, we found that wild pig foraging sites do not appear to be associated with any specific plant group or origin status (native or non-native) within the secondary forests of Singapore. Our work is situated within secondary forests so that the knowledge gained can help inform Singapore's substantial reforestation efforts and specifically help to restore or protect habitats from wild pig degradation.

Introduction

Wild pigs (*Sus scrofa*) were extirpated from mainland Singapore in the 1950s but they have recolonised the island in the early 2000s and their range and density have since increased (Figure 1; Khoo et al., 2021; Koh et al., 2018; Yong et al., 2010; Corlett, 1992). In Southeast Asia, large wild pig populations have been shown to negatively impact forests soils, limit tree regeneration through seed predation, digging up seedlings and sapling roots, and breaking





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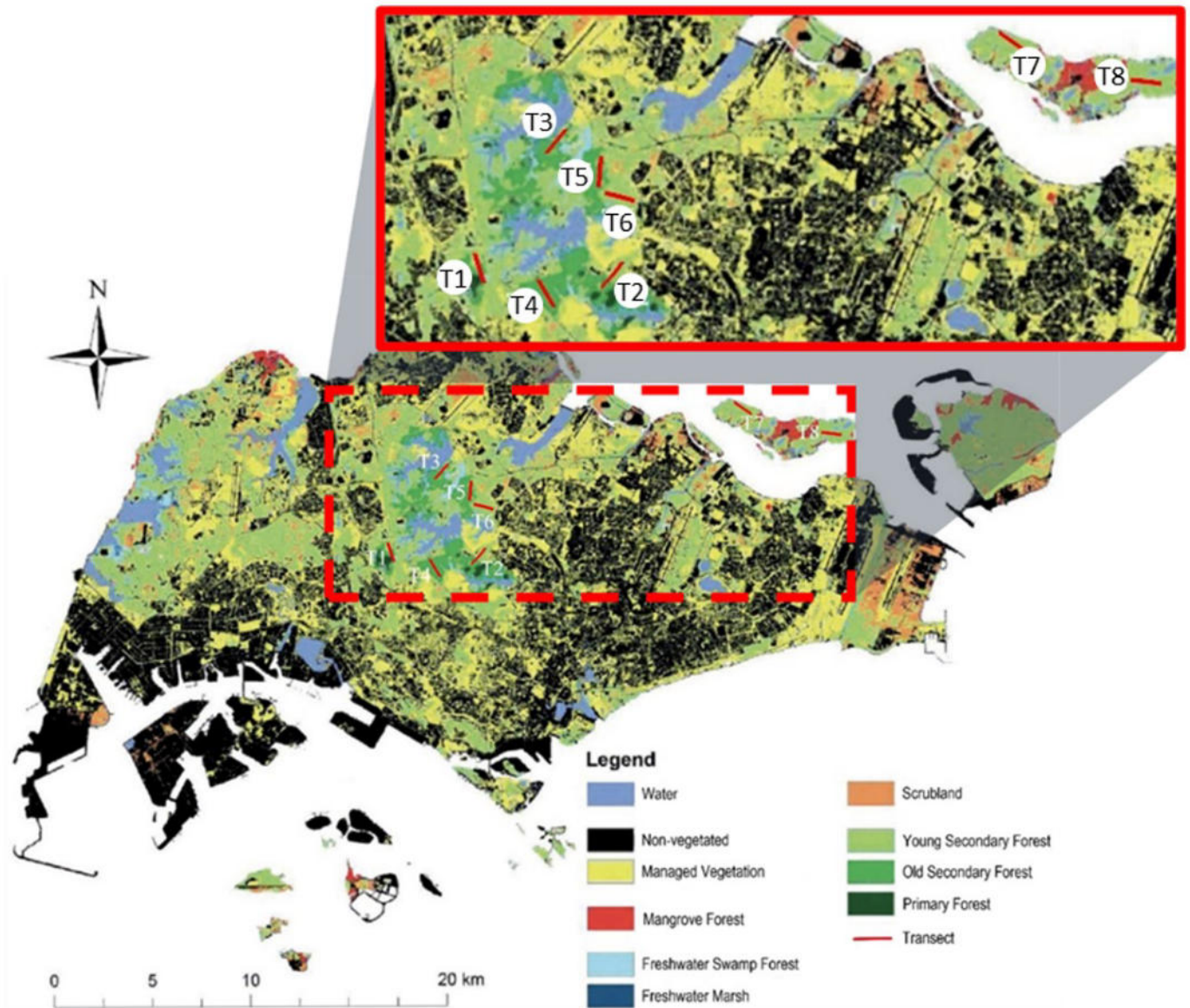


Fig. 2: Locations of eight flora and pig foraging transects surveyed across secondary forests in Singapore. Map adapted from Yee et al., 2011.

saplings to construct their birthing nests, and even reduce forest carbon storage (Luskin et al., 2021; O'Bryan et al., 2021; Williams et al., 2021; Luskin et al. 2019; Wehr et al., 2018, Luskin et al., 2017; Yong et al., 2010; Ickes et al., 2001). Furthermore, the suppression of native plant species recruitment and increased disturbance to soils, coupled with wild pigs as seed dispersers, may increase opportunities for non-native plant species to invade the forests (Wehr et al., 2018; Dovrat et al., 2012; Fujinuma and Harrison, 2012; Yong et al., 2010).

Wild pigs generally have diverse omnivorous diets including a large proportion of plant matter (Senior et al., 2016). Many studies outside of Singapore showed that wild pigs prefer certain types of plants (e.g., oak, legumes, agricultural crops), which is largely influenced by food availability, energy and nutrient content (Kim et al., 2019; Lee & Lee, 2019; Luskin et al., 2017; Rivero et al., 2017; Ballari & Barrios-García, 2014; Giménez-Anaya et al., 2008; Schley & Roper, 2003). Previous work in the nearby Pasoh forest (Peninsular Malaysia) found that wild pig habitat preferences and disturbances strongly altered tree diversity and favoured lianas over trees (Luskin et al., 2021; Luskin et al., 2019; Ickes et al., 2005). However, those studies focused on





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the family-level plant composition and did not investigate differences in specific plant genera or non-native versus native plant species. In this study, we investigated if particular types of plants were associated with wild pigs foraging sites in Singapore's secondary forests. Specifically, we explored whether they prefer a specific genus or genera of plants over others, and non-native over native plant species.

Our work is situated within secondary forests so that the knowledge gained can help inform Singapore's substantial reforestation efforts and specifically help to restore or protect habitats from wild pig degradation.

Methods

Study Area

Singapore comprises of 19.64% young secondary forest and 1.37% old secondary forests in terms of land area (Yee et al., 2011). It is estimated that non-native species account for 44% of the total vascular flora in Singapore, with 18% growing in the wild and 12% being regarded as fully naturalised (Nghiem et al., 2015; Chong et al., 2009).

Our work documenting the flora nearby pig foraging sites occurred in a mosaic of secondary forests (native-dominated forests and abandoned-land secondary forests) in the Bukit Timah Nature Reserve, Central Catchment Nature Reserve and Pulau Ubin island in December 2020 (Figure 2). We surveyed 2-3 randomly located 6 m (W) × 1000 m (L) straight-line transects in each of the three areas (eight in total).

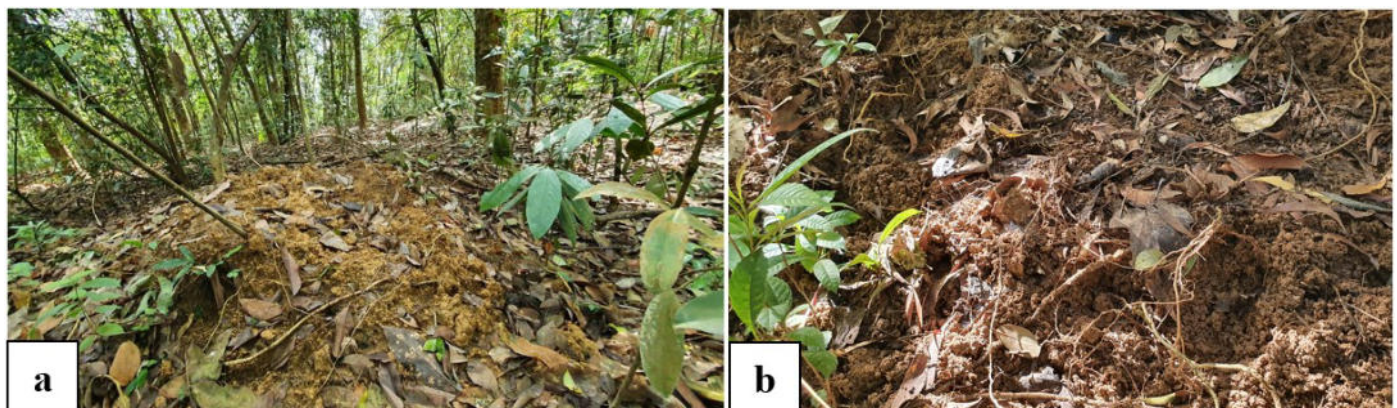
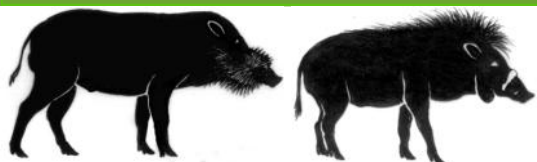


Fig. 3: Examples of a wild pig foraging sites, which are characterised by the exposed soil and roots. We assessed the plant community within a 1-m radius of foraging sites (a). Most foraging activities observed appeared to target roots (b). Photos: C. Yong.

Study species

Wild pigs (also called wild boars) are common throughout Southeast Asia. Their recent population rise in Singapore is partly due to the absence of tigers (*Panthera tigris*), their natural apex predator (Khoo et al., 2021; Koh et al., 2018; Yong et al., 2010). Additionally, Singapore's ban on hunting also strongly supports pig densities, similar to nearby areas of Malaysia and Indonesia where hunting is limited due of the Halal diet restrictions on pork (Luskin et al., 2014). This leaves Singapore's pig populations to be largely limited by the availability of food and suitable habitat (Khoo et al., 2021). These factors are not independent; predator loss, low hunting, and anthropogenic food subsidies act synergistically to determine pig densities. For example, the wild pig density in Southeast Asian forests that lack large predators, like Singapore, was projected to be ten times that of forests with large predators (Yong et al., 2010; Ickes et al., 2005). However, in





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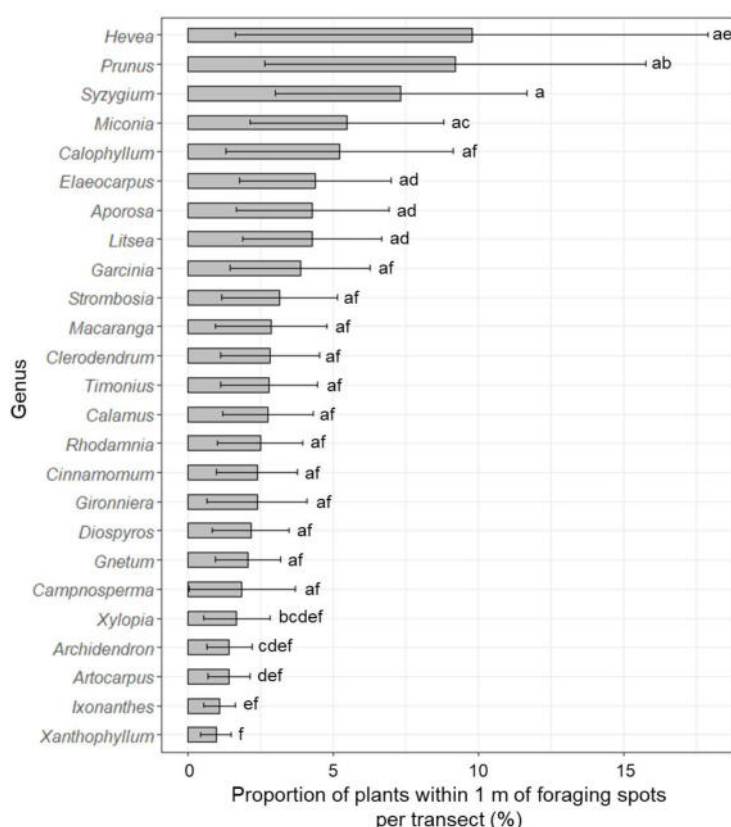


Fig. 4: Percentage of individuals of common plant genera recorded within 1-m radius of wild pig foraging sites. Bars are means and error bars represent 95% confidence intervals from a linear mixed effects model (Table 1. Different letters across genera indicate significant differences (post hoc Tukey test, $P \leq 0.05$).

Statistical Analysis

We used linear mixed-effects models (LME) (Pinheiro & Bates, 2000) to compare differences in the proportion of plants near/within foraging sites among the selected common plant genera, with ‘plant genus’ treated as the fixed factor and the ‘transect location’ as a random factor. Additionally, LME models were used to compare differences in the proportion of native and non-native species found near/within foraging sites, with ‘plant origin status’ as the fixed factor and the ‘transect location’ as a random factor.

To ascertain model assumptions, standardised residuals were plotted and visually inspected. The model with the most appropriate variance structure was selected using sample-size adjusted Akaike Information Criterion values and likelihood-ratio tests (Zuur et al., 2009). Post hoc Tukey tests were conducted when the factor of interest of the selected LME model showed significant differences (Hothorn et al., 2008). All statistical analyses were conducted using ‘R’ version 4.0.5 (R Core Team, 2021) using ‘NLME’ (Pinheiro et al., 2014) and ‘MULTCOMP’ (Hothorn et al., 2008) packages.

Results

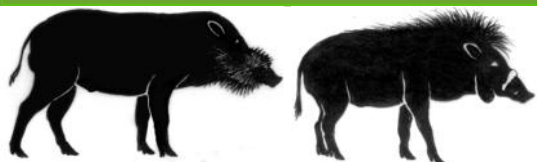
In total, 96 plant genera were recorded within 1 m of wild pig foraging sites across all eight

forests without tigers, where pig hunting is limited, and where pigs can access food subsidies like crops or trash, pig densities can increase 100-fold relative to intact or hunted forests (Luskin et al., 2017). Soil disturbance by wild pig foraging behaviour is characterized by uneven surfaces of loose soil that have no litter layer or vegetation cover left from pigs turning the soil over (Figure 3). Singapore does not have any other animals that disturb the soil in this particular manner.

Flora associated with pig disturbances

We recorded all signs of foraging activity by wild pigs along randomly located 1 km straight-line transects with a 6 m wide observation window (3 m left and right). We recorded the plants within a 1 m radius of each foraging site, identified to genus and, if possible, species level. We calculated the percentage of each genus and the native versus non-native plants out of the total plant individuals per transect. We assumed that understorey plants in the pig foraging sites may have contributed towards the wild pig diet.





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transects. Twenty-five plant genera were recorded in at least four of the eight transects, but all 25 genera showed low occurrences (below 10% of individuals) and most showed statistically similar occurrences to each other (Figure 4; Table 1).

Native plants accounted for 89% of plant individuals (Figure 5; Table 1). The most common non-native species documented near foraging sites were hairy clidemia (*Miconia crenata*, syn. *Clidemia hirta*) and rubber (*Hevea brasiliensis*).

Discussion

Comparison across common plant genera

We found no patterns in plant associations with wild boar disturbances. This may differ from studies in other countries that found plant associations within wild pig diets. For example, pigs preferred oak over conifers in Korea (Lee & Lee, 2019), leguminous plants over grasses in Chile (Rivero et al., 2017), and agricultural crops (e.g., oil palm) over forest species in Malaysia (Luskin et al., 2017). The low density of energy-rich plants (e.g., legumes, oil palm) within our surveyed transects may have led pigs to utilise all possible nearby food sources and consume readily available subsurface material.

Many of the common plant species recorded in our study are also commonly found in previous vegetation surveys of Singapore's young and old secondary forests, which can be further classified into native-dominated and abandoned-land forests (Yee et al., 2016; Chua, 2014; Neo et al., 2014). Hence, our results may be reflective of the vegetation composition of Singapore's secondary forests rather than indicative of any plant preference by the pigs. Moreover, wild pigs may have adapted to utilising energy-rich urban plants, such as yam, tapioca and oil palm, which are more abundant at the urban-forest interface outside of our study area (NSS, 2012). As such, future studies could analyse wild pig faecal samples for plant DNA composition and seed content to give a more accurate representation of what they prefer to eat, and this would serve to remove the spatial constraints of line transect sampling.

Comparison across native and non-native plants

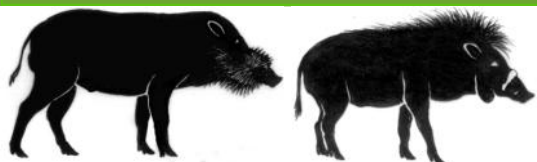
The high occurrence of hairy clidemia near or within wild pig foraging sites could be attributed to its inherently invasive nature. Wild pig foraging activities turn over the soil, which facilitates colonisation of the site by this pioneer shrub that is known to prefer disturbed soils and canopy gaps with abundant light (Fujinuma & Harrison, 2012; Peters, 2001). On the other hand, the high occurrence of rubber plants is reflective of how it was the favoured crop for cultivation for the most recent wave of plantation agriculture (Corlett, 1992; Dobby, 1940).

Rubber plants are potentially an important supplementary food source for the wild pigs because mature trees tend to produce high numbers of seedlings and fruits (which are produced twice a year), and their shade-tolerant seedlings show high recruitment rates (Nghiem et al., 2015; Yeang, 2007). Further studies could assess if the removal of rubber trees from secondary forests can indirectly control the wild pig population. However, much care should be taken to ensure that

Tab. 1: Test statistics of one-factor linear mixed-effects models (LME) to test for the differences in percentages of plant individuals occurring near foraging sites among different common plant genera (a) and between native and non-native plants within a transect (b). Transect location was considered as a random factor for each model. Significant P values ($P \leq 0.05$) are presented in bold.

| | d.f. (n, d) | F-value | P-value |
|--|-------------|---------|----------------|
| (a) Proportion of common plant genera | 24, 120 | 3.0310 | < 0.001 |
| (b) Proportion of native/non-native plants | 1, 7 | 319.814 | < 0.001 |





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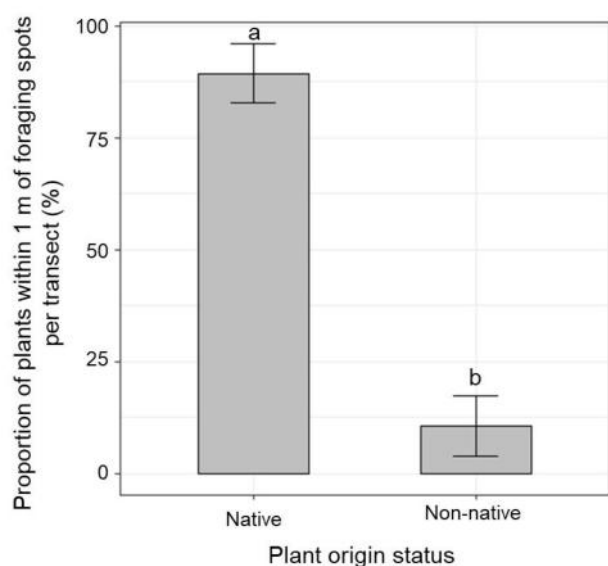


Fig. 5: Percentage of native and exotic plants recorded within 1-m radius of wild pig foraging spots. Bars are means, and error bars represent 95% confidence intervals from a linear mixed effects model. (Table 1. Different letters across genera indicate significant differences (post hoc Tukey test, $P \leq 0.05$).

non-native plant species (Yee et al., 2011, 2016). Future studies could conduct comprehensive vegetation surveys and diet analyses to determine how pigs influence plant composition of non-native species. Finally, with the lethal onslaught of African Swine Fever likely to reach Singapore in the near future, there are opportunities for natural 'before-and-after' studies to examine pigs influence on the environment (Luskin et al., 2020).

Conclusion

Our study provided insights into the foraging habits of wild pigs in Singapore secondary forests. Contrary to studies in other countries that indicated wild pigs show preference for certain types of plants over others, our study found that wild pigs in Singapore showed no distinct preference for any common genus or for non-native or native plants within Singapore secondary forests.

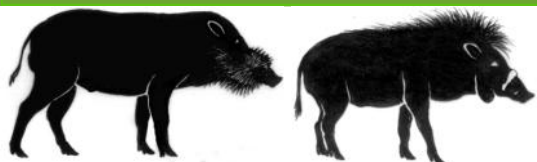
Acknowledgements

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References

- Ballari SA and Barrios-García MN. 2014. A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. *Mammal Review* 44(2): 124–134.
- Chua SC. 2014. Fate, luck or destiny? Regeneration of tropical rainforest in Singapore. University of California Berkeley.
- Corlett RT. 1992. The Ecological Transformation of Singapore, 1819-1990. *Journal of Biogeography* 19(4): 411-420.
- Chong KY, Tan HTW and Corlett RT. 2009. A checklist of the Total Vascular Plant Flora of



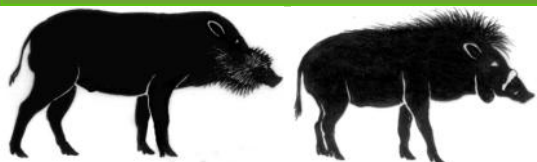


Ecology and Conservation



- Singapore: Native, Naturalised and Cultivated Species. Raffles Museum of Biodiversity Research, National University of Singapore.
- Dobby EHG. 1940. Singapore: Town and Country. Geographical Review 30(1): 84–109.
- Dovrat G, Perevolotsky A and Ne'eman G. 2012. Wild boars as seed dispersal agents of exotic plants from agricultural lands to conservation areas. Journal of Arid Environments 78: 49–54.
- Fujinuma J and Harrison RD. 2012. Wild Pigs (*Sus scrofa*) Mediate Large-Scale Edge Effects in a Lowland Tropical Rainforest in Peninsular Malaysia. PLoS One 7(5): e37321.
- Giménez-Anaya A, Herrero J, Rosell C, Couto S and García-Serrano A. 2008. Food habits of wild boars (*Sus scrofa*) in a Mediterranean coastal wetland. Wetlands 28(1): 197–203.
- Hothorn T, Bretz F and Westfall P. 2008. Simultaneous Inference in General Parametric Models. Biometrical Journal 50(3): 346–363.
- Ickes K, Dewalt SJ and Appanah S. 2001. Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. Journal of Tropical Ecology 17(2): 191–206.
- Ickes K, Paciorek CJ and Thomas SC. 2005. Impacts of nest construction by native pigs (*Sus scrofa*) on lowland Malaysian rain forest saplings. Ecology 86(6): 1540–1547.
- Khoo MDY, Lim BTM, Soh MCK, Loy RHY, Lua HK., Lee BPYH, Loo AHB and Er KBH. 2021. Persistence of a locally endangered mouse-deer amidst the re-emergence of two larger ungulates in small urban rainforest fragments. Global Ecology and Conservation 30: e01807.
- Kim Y, Cho S and Choung Y. 2019. Habitat preference of wild boar (*Sus scrofa*) for feeding in cool-temperate forests. Journal of Ecology and Environment 43(3): 297–304.
- Koh JJM, Webb EL and Leung LKP. 2018. Using a spatial mark-resight model to estimate the parameters of a wild pig (*Sus scrofa*) population in Singapore. Raffles Bulletin of Zoology 66: 495-505.
- Lee SM and Lee EJ. 2019. Diet of the wild boar (*Sus scrofa*): Implications for management in forest-agricultural and urban environments in South Korea, PeerJ 7: e7835.
- Luskin MS, Christina ED, Kelley LC and Potts MD. 2014. Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia. Human Ecology 42: 35–45.
- Luskin MS, Brashares JS, Ickes K, Sun, IF, Fletcher C, Wright SJ and Potts MD. 2017. Cross-boundary subsidy cascades from oil palm degrade distant tropical forests. Nature Communications 8: 2231.
- Luskin MS, Ickes K, Yao TL and Davies SJ. 2019. Wildlife differentially affect tree and liana regeneration in a tropical forest: An 18-year study of experimental terrestrial defaunation versus artificially abundant herbivores. Journal of Applied Ecology, 56(6), 1379–1388.
- Luskin MS, Meijaard E, Surya S, Walzer C, Linkie M. 2020. African Swine fever threatens Southeast Asia's 11 endemic wild pig species. Conservation Letters e12784.
- Luskin MS, Ickes K, Davies S, Johnson D and Leong YT. 2021. Wildlife disturbances as a source of conspecific negative density dependent mortality in tropical trees. Proc. R. Soc. B. 288: 20210001.
- Ministry of National Development (MND). 2017. Written Answer by Ministry of National Development on wild boar sightings.
- Nature Society (Singapore) (NSS). 2012. Nature Society (Singapore)'s Position Paper on Wild





Ecology and Conservation



Pigs in Singapore.

- Neo L, Yee ATK, Chong KY, Yeoh YS and Tan HTW. 2014. The vascular plant flora of abandoned plantations in Singapore IV: Windsor Forest. *Nature in Singapore* 7: 93-109.
- Nghiem LTP, Tan HTW and Corlett RT. 2015. Invasive trees in Singapore: Are they a threat to native forests? *Tropical Conservation Science*, 8(1): 201–214.
- O’Bryan CJ, Patton NR, Hone J, Lewis JS, Berdejo-Espinola V, Risch DR, Holden MH and McDonald-Madden E. 2021. Unrecognized threat to global soil carbon by a widespread invasive species. *Global Change Biology* 28(3), 877–882.
- Peters HA. 2001. *Clidemia hirta* invasion at the Pasoh Forest Reserve: An unexpected plant invasion in an undisturbed tropical forest. *Biotropica*, 33(1): 60–68.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S, Van Willigen BV and Ranke J. 2014. nlme: Linear and nonlinear mixed effects models (R package version 3.1 128).
- Pinheiro J and Bates D. 2000. *Mixed-Effects Models in S and S-PLUS*. 1st edn. Springer-Verlag New York.
- R Core Team. 2021. R version 4.0.5 (Shake and Throw).
- Rivero MJ, Gallardo MA, Marnet PG and Velásquez A. 2017. Dietary preference of European wild boar (*Sus scrofa* L.) grazing grass and legume at two contrasting plant heights: A pilot study. *Livestock Science* 200: 64–70.
- Schley L and Roper TJ. 2003. Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review* 33(1): 43–56.
- Senior AM, Grueber CE, Machovsky-Capuskaa G, Simpson SJ and Raubenheimer D. 2016. Macronutritional consequences of food generalism in an invasive mammal, the wild boar. *Mammalian Biology* 81(5): 523–526.
- Srivathsan A, Ang A, Vogler AP and Meier R. 2016. Fecal metagenomics for the simultaneous assessment of diet, parasites, and population genetics of an understudied primate. *Frontiers in Zoology* 13(1), 17.
- Wehr NH, Hess SC and Litton CM. 2018. Biology and Impacts of Pacific Islands Invasive Species. 14. *Sus scrofa*, the Feral Pig (Artiodactyla: Suidae). *Pacific Science* 72(2): 177–198.
- Williams PJ, Ong RC, Brodie JF and Luskin MS. 2021. Fungi and insects compensate for lost vertebrate seed predation in an experimentally defaunated tropical forest. *Nature Communications* 12:1650-1671.
- Yeang HY. 2007. Synchronous flowering of the rubber tree (*Hevea brasiliensis*) induced by high solar radiation intensity. *New Phytologist* 175(2): 283–289.
- Yee ATK, Corlett RT, Liew SC and Tan HTW. 2011. The vegetation of Singapore - An updated map. *Gardens’ Bulletin Singapore* 63(1 & 2): 205–212.
- Yee ATK, Kwek YC, Neo L and Tan HTW. 2016. Updating the classification system for the secondary forests of Singapore. *Raffles Bulletin of Zoology* 32: 11–21.
- Yong DL, Lee BPHY, Ang A and Tan KH. 2010. The status on Singapore Island of the Eurasian Wild Pig *Sus scrofa* (Mammalia: Suidae). *Nature in Singapore* 3: 227–237.
- Zuur AF, Ieno EN, Walker N, Saveliev AA and Smith GM. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

